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An Approach to Functionalizing Key Environmental Factors Forage Production in Rocky Mountain Aspen Populus-Tremuloides Stands

J.P. Roise

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confidence bands give the researcher an indication of the uncertainty associated with extrapolation outside that region in which the data were collected.

One of the future uses of the litter decomposition model, for example, might be to predict the age distribution of the leaf litter on the forest floor by calculating the undecomposed portion of litter from a number of years. Propagating this error through time in a simulation should result in some measure of the reliability of the results and thus increase the amount of information to be obtained from the available data and the simulation analysis.

The procedures discussed here may be applied to those component functions whose parameters are estimated from experimental or observational data. Techniques need to be developed that will allow incorporation of confidence information or subcomponent functions to be extended throughout the structure of the model. Eventually some confidence statement on the final system predictions may be obtainable by these procedures. In fact, as pointed out by one of the reviewers, such procedures are already in development.

ACKNOWLEDGMENTS

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AN APPROACH TO FUNCTIONALIZING KEY ENVIRONMENTAL FACTORS: FORAGE PRODUCTION IN ROCKY MOUNTAIN ASPEN STANDS

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ABSTRACT

Roise, J.P., Betters, D.R. and Kent, B.M., 1981. An approach to functionalizing key environmental factors: forage production in Rocky Mountain aspen stands. *Ecol. Modelling*, 14: 133–146.

An approach is discussed for developing production functions which exhibit logical interrelationships between growth factors in a biological system. Functional relationships are hypothesized for growth factors involving available moisture and energy. These growth factors are, in turn, related to site variables which influence their availability. Both linear and non-linear regression techniques are used to identify key site variables and appropriate functional forms. These models involving growth factors are then synthesized into one equation to estimate forage production. The production equation illustrates the implied relationship between topographic variables such as elevation and aspect, soil variables such as water holding capacity, and timber stand density on the moisture and energy growth factors.

INTRODUCTION

This paper discusses both a conceptual approach for developing functional forms of biophysical production models and the application of this approach to the construction of a forage production model for Rocky Mountain aspen (*Populus tremuloides* Michx.) stands. Typically, forest ecosystem yields are influenced by many growth factors, and production is difficult to predict due to the diversity and complexity of the environmental influences. Because of this diversity, purely empirical 'prediction' models using only site variables have often been of limited value. Further, other approaches, such as habitat typing and site indexing, are not descriptive of interactions since they sum the physical environment into plant responses or communities, and do not directly account for interaction between growth factors and site conditions. As an alternative, semi-empirical models, that is, biomathematical models which depict meaningful functional relationships between growth factors, may be useful in providing more accurate representation of production functions (Pienaar, 1966). These models are normally more complex mathematically and difficult to develop, since the modeler must be knowledgeable about the biophysical functional relationships in order to describe them in a mathematical format. The approach used in this study illustrates how a model can be developed to depict functional forms that exhibit logical interrelationships within a biological production system. This model may be used for predicting as well as illustrating logical relationships between the growth factors that affect production.

FORAGE PRODUCTION IN ASPEN STANDS

Aspen forests occupy more than 2.2×10^6 ha in the Rocky Mountain region. Existing on a wide range of site conditions, the species is one of the most diverse forest types in the United States. Aspen forests have many uses, including the production of forage. In comparison to other forests in the Rocky Mountain region, aspen stands typically produce more forage in the understory, making such stands particularly important for domestic livestock, wildlife and firebreak uses (Jones, 1973).

Given the diversity in aspen stand characteristics, topography and soil conditions, models to predict forage production have been difficult to develop. Most efforts have concentrated on constructing empirical models that use only one or two variables. Most of these studies have related forage production to overstory variables only, and there have been conflicting conclusions. For example, Alway and Kitteridge (1933), Harper (1973) and Severson and Kranz (1976), concluded there was no relationship between the aspen overstory and the understory production, while Ellison and Houston (1958) and Reynolds (1969) indicated the overstory did have an effect. These authors and others have suggested that there are other significant site characteristics besides the overstory that may influence forage production.

GROWTH FACTORS, SITE VARIABLES AND FUNCTIONAL FORMS

Aspen plant communities typically have an intermingling of growth factors, where no one factor is limiting (Kitteridge, 1938). In the Rocky Mountains there is considerable variation in these factors due to rough terrain. In particular, such terrain influences the growth factors of temperature, available moisture and length of the growing season (Fritts, 1976). Site variables such as aspect, elevation, latitude and slope largely determine the length of the growing season and the temperatures found on aspen sites

(Langenheim, 1962; Morgan, 1969). Available moisture in aspen stands is also affected by these topographic variables as well as by the site's soils (Ellison and Houston, 1958). Thus, growth factors can be related to a set of site variables. For example, the influence of soils on the growth factor available moisture may be described by site variables dealing with soil particle size and/or percent organic matter.

To build logical functional relationships between production, growth factors, and site variables, one might apply the law of relative effects suggested by Lundegardh (1931). Basically, the law states that if one growth factor is limiting, then no increase in other growth factors can adequately compensate for the deficiency. If this is the case, the factors in a mathematical function should be multiplicative. That is, the growth factors are modeled by an equation where they are multiplied by one another, so when one becomes 'limiting', no further increase in another will augment production. This modeling technique is basically the same as the multiplicative environmental effects discussed by Botkin et al. (1972) and Reed (1980). If, on the other hand, a particular growth factor does not solely limit production, then the factor would be additive in a mathematical sense.

THE HYPOTHESIZED MODELS

These basic concepts concerning growth factors and means of expressing logical relationships were applied to hypothesize the initial model:

$$Y = A \exp[F_1(X_1)] \exp[F_2(X_2)] = A \exp[F_1(X_1) + F_2(X_2)] \tag{1}$$

where Y is the forage production in kg ha^{-1} with growth factors, X_1 is the available moisture and X_2 is the available energy. In this case, only two growth factors were considered, available water and available energy. Other growth factors, such as nutrients, were not used since previous research indicated they were not, for the most part, limiting growth factors in the area studied (Jones, 1967). The growth factors, X_1 and X_2 are conceptualized as average values for the entire growing season and are made up of a composite of inputs. For example X_1, available moisture, includes precipitation, evapotranspiration and soil water; while X_2, available energy, includes light, ambient energy and temperature inputs. It is realized that the growth rates can vary quite markedly on a shorter time basis (e.g. daily), but for purposes here (and data available) total growing season and a broad definition of the growth factors is an appropriate level of resolution.

The production function (eq. 1) form was chosen since it allows for the multiplicative influence of the growth factors. The function also provides for the additive characteristics concerning site variables. For example, $F_1(X_1)$ or $F_2(X_2)$ may include several site variables added together. The exponential

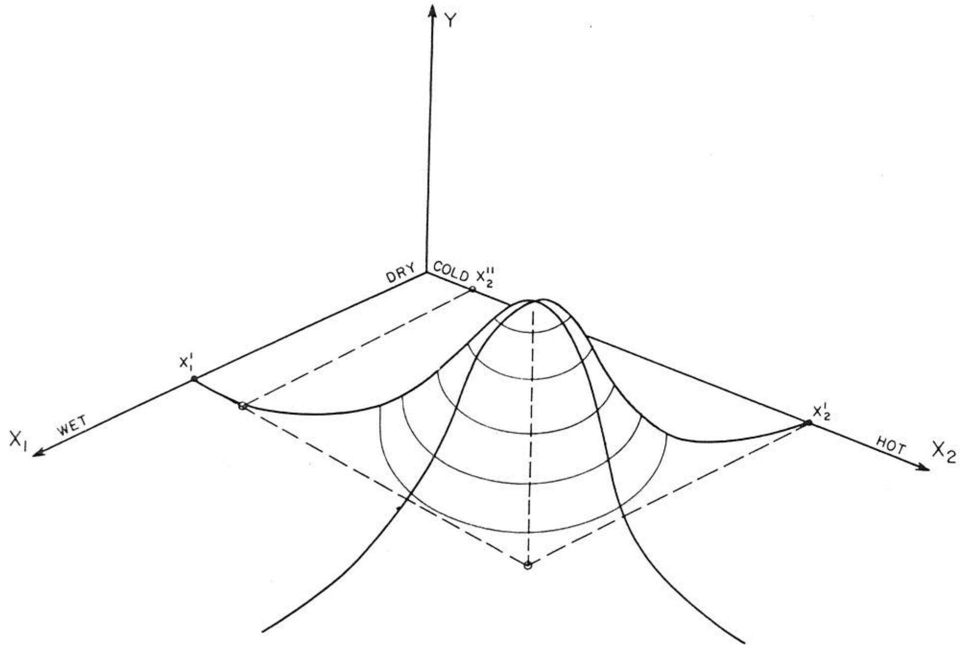

Fig. 1. Forage production (Y) conceptualized as a function of water and energy availability. Maximum production occurs at X_1', X_2'.

form used also allows for the common 'bell-shaped' relationship between production and a growth factor. And the form provides a function that can easily handle large numbers of variables and be linearized to allow use of linear regression techniques.

The generalized production function (eq. 1), as pictured in Fig. 1, reaches a maximum value for some combination of growth factors (X_1', X_2'). If X_2, available energy, is at X_2'' and available moisture, X_1 is X_1' then energy is the limiting growth factor. Similar type interpretations could be made for other points on the production surface. In the geographic region under study, generally both water and energy are in short supply, less than X_1', X_2'.

These growth factors can be related to measurable site variables. The functional forms and variables utilized in this study were based on evaluation and collation of the results of previous studies (cited earlier) related to the identification and quantification of biophysical interrelationships in aspen. In forming the hypothesized models, particular emphasis is given to the influence of topography on the growth factors. Rocky Mountain aspen, because of the mountainous terrain, is located on a wider range of topographic conditions. Various researchers have recognized the importance of topography (Langenheim, 1962; Reed, 1971; Severson and Thilenius, 1976). Several researchers have constructed model transformations concerning

specific parameters such as slope or aspect (Trimble and Weitzman, 1956; Beers et al. 1966; Stage, 1976). The model of Beers et al. (1966) is a generalized version of Trimble and Weitzman's (1956) formula. The topographic transformation developed in this study is a further generalization of the Beers et al. transformation and is utilized to account for changes in available energy as a function of elevation and aspect. While Beers et al.'s transformation used only one independent variable, aspect, the function developed here uses both aspect and elevation. To develop the function concerning the relationship between available energy, aspect and elevation, $X_2 = g_1$ (topography), two assumptions were made:

Assumption 1

As elevation increases available energy (X_2) decreases. Higher elevations have lower average temperatures and lower ambient energy levels. In this case, a decreasing linear function is hypothesized

$$X_2 = b_0 - b_1 Z_1 \tag{2}$$

where Z_1 is the elevation in meters.

Assumption 2

Available energy is directly related to the amount of incident solar radiation, and the aspect angle (radians) is a major factor influencing the amount of solar radiation. Available energy is at a maximum at some aspect, A_{max}. As the aspect angle moves away from A_{max}, available energy decreases. The following hypothesized relationship is therefore defined between energy and aspect

$$X_2 = b_2 \cos(A_{max} - Z_2) \tag{3}$$

where Z_2 is the aspect in radians.

When the aspect of the site is equal to A_{max} (i.e. $Z_2 = A_{max}$), then the value of the cosine function is equal to unity, its maximum value. As the aspect angle moves away from A_{max} the value of the X_2 decreases. When aspect is π radians away from A_{max}, the cosine function is at its minimum value. The magnitude of the effect of aspect on X_2 can be small or large, depending on the value of b_2.

Equations 2 and 3 are set equal and solved for A_{max} as a function of elevation. Thus the optimal aspect angle is expressed as a function of elevation alone

$$b_0 - b_1 Z_1 = b_2 \cos(A_{max}) \tag{4}$$

and solving for A_{max}

$$A_{max} = \arccos\left(\frac{b_0 - b_1 Z_1}{b_2}\right) \tag{5}$$ *

Now expressed as a function of elevation, A_{max} is an angle of constant available energy. As elevation changes, A_{max} also changes, in such a way that available energy remains the same.

Substituting this value for A_{max} into eq. 3 yields the hypothesized equation for available energy

$$X_2 = b_0\left[\cos b_1 \arccos\left(\frac{b_2 - Z_1}{b_3}\right) - Z_2\right] \tag{6}$$

Through this expression for X_2, the effects of aspect and elevation are related to energy.

The growth factor X_1's functional form and measurable site variables are initially hypothesized as

$$X_1 = g_2\,(\text{vegetation, topography, soil})$$

$$X_1 = (b_0 + b_1 Z_1 - b_3 Z_3 + b_4 Z_4 + b_5 Z_5 - b_6 X_2)\{1/[b_7 + b_8 \exp(-b_9 Z_6)]\} \tag{7}$$

where Z_1 is the elevation (m); Z_2 is the aspect (rad.); Z_3 is the number of stems per hectare; Z_4 is the soil particle size (μm); Z_5 is the organic matter in soil (%); and Z_6 is the soil depth to an impermeable layer (m).

For X_1, the expression for available moisture, there is an implied interaction between moisture and energy. The function (eq. 7) is written so that moisture, X_1, is partially dependent on energy, X_2. As the available energy increases the potential evapotranspiration rate is expected to increase, and therefore this increases the loss of moisture. Further, available moisture is influenced by other vegetative, soil and topographic site characteristics (Z_1–Z_6). Whereas in the production function (eq. 1) the site factors X_1 and X_2 were multiplicative, in eq. 7, Z_1, Z_3, Z_4, Z_5 and X_2 are all additive. A favorable value for any one of these can increase available moisture, but an unfavorable value will not, in itself, limit available moisture.

The expression for X_1 summarizes the effects of topographic, edaphic and biotic environments on available moisture. At this point, the site variables included were those thought most significant to each of the three environmental components, vegetation, topography and soil. 'Significance', at this stage, was determined on the basis of past research results. Later, statistical analysis may point to some variables being insignificant for this study area and/or other variables being more significant than those initially included.

* For a more detailed discussion concerning this functional form see Roise, J.R. and Betters, D.R., An aspect transformation with regard to elevation for site productivity models, a manuscript accepted for publication, 11 February 1981, by Forest Science.

IDENTIFYING THE MOST CRITICAL SITE VARIABLES

In developing any model, and in particular a more mathematically complex model, it is desirable to limit the number of variables, including only those of key importance. This identification of key variables normally requires the use of covariance analysis and regression techniques. While these statistical techniques provide an analytical measure for selecting variables from a data base, they should not be the sole criteria. The knowledge and experience of the modeler should also be utilized to complete this phase.

In order to test the hypothesized relationships and to construct a final production equation, both a secondary and a primary data set was utilized. Table I lists the site variables measured. These data relating to aspen stand-site characteristics were collected from the Routt National Forest in Colorado during the summer of 1978. A total of 41 sample plots were established. The plots were located using topographic, timber type and geological surface maps. Forage samples were collected by using wire cages on each plot. Variables measured included: a composite soil sample involving percent organic matter, soil depth, soil particle size and color of the A and B horizon; topographic variables relating to aspect, slope, position on the slope and elevation; stand variables, including basal area and stems per hectare. Soil samples were tested by the hydrometer method for particle size distribution. Moisture tension tests were made at 0, 1–3, and 1–15 bars. The forage sample was dried at 105°C for a period of 24 h.

In the case of the primary data, multiple linear regression was used to examine various sets of site variables and determine those sets which had the highest correlation to forage production. To ensure that site variables were not deleted if they indicated non-linear instead of linear relationships, several linear transformations were utilized, as well as non-linear regression techniques. For example, aspect was transformed using a simple sine function, $A' = \sin(A)$, where A' is the transformed aspect code and A is the measured aspect angle. Forage production was transformed to a natural logarithm, $Y' = \ln Y$, where Y' is the transformed understory code and Y is the measured understory production. Different soil particle size variables were squared to test the possibility of non-linear relationships between water holding capacity and soil texture. After testing sets of possibilities for variables, the analysis indicated that the set of soil color, water holding capacity, aspect, elevation and stems per hectare was most highly correlated to forage production.

TABLE I

Site factors (Z_i) measured in collection of primary data

Forage factors	Stand factors	Topographic factors	Soil factors
Weight of forage	Number of stems	Slope	Weight at 1 bar
Weight of shrubs	Average basal area	Aspect	Weight at 1—3 bars
Weight of forbs	10 in.-diameter class	Position on slope	Weight at 15 bars
Weight of grasses	12 in.-diameter class	Elevation	Change in weight between 1 and 15 bars
Percent of shrubs	14 in.-diameter class		Change in weight between 1-3 and 15 bars
Percent of forbs	16 in.-diameter class		Change in weight between 1 and 15 bars
Percent of grasses	18 in.-diameter class		Percent of soil particles sized 5 μm and less
	20 in.-diameter class		Percent of soil particles sized 10 μm and less
	Range in ages		Percent of soil particles sized 20 μm and less
	Growth rate for last 10 years		Percent of soil particles sized 50 μm and less
	Average growth rate		Color of A horizon
	Average DBH		Color of B horizon
	Basal area h^{-1}		Parent material
	Stem spacing		Depth of A horizon
	Regeneration		Depth of B horizon
	Height of dominants		
	Age of dominants		
	Site index		
	2 in.-diameter class		
	4 in.-diameter class		
	6 in.-diameter class		
	8 in.-diameter class		

In addition to this primary data analysis, secondary data available from Warner and Harper's (1972) study were also analyzed to identify significant site variables. Their study considered 40 plot measurements for both stand and site characteristics. The correlation matrix for their data indicated that a correlation, though weak, exists between forage production and the site variables aspect and elevation. This helped to confirm the use of these variables for the next step in modeling.

Not all the variables originally hypothesized were used in the final production model. For example, 'depth to the impermeable layer' in soils was found to be statistically non-significant. This is probably a result of the area studied and its data set. None of the sites sampled had shallow soil, thus soil depth was never a major limiting factor. Another data set developed around a wide range of soil depth samples would probably indicate different results. This implies that the model is most applicable to areas where the limiting site variables are those included in the model.

Other hypothesized variables were changed by substituting site variables measuring similar characteristics. For example, percent organic matter in the soil was replaced by color of the A and B horizon, and soil particle size was replaced by soil field capacity. These variables indicated a higher correlation to production than the initially hypothesized parameters.

THE PRODUCTION MODEL

After examining the data base to determine the most significant sets of site variables, eqs. 6 and 7 were modified to include only those site variables found significant

$$X_1 = b_0 - b_3 Z_3 + b_7 Z_7 + b_8 Z_8 + b_9 Z_9 - b_6 X_2$$

$$X_2 = b_{10} \cos\left[\arccos\left(\frac{b_{11} - Z_1}{b_{12}}\right) - Z_2\right] \qquad (8)$$

where Z_7 is the color of the A horizon, Z_8 is the color of the B horizon and Z_9 is the soil field capacity in grams.

The final model is developed by substituting eq. 8 into eq. 1 to form the production function

$$Y = A \exp(b_0 - b_3 Z_3 + b_7 Z_7 + b_8 Z_8 + b_9 Z_9 - b_6 X_2) \exp(X_2)$$

which can be reduced to

$$Y = A \exp(b_0 - b_3 Z_3 + b_7 Z_7 + b_8 Z_8 + b_9 Z_9) + b_{10}\left\{\cos\left[\arccos\left(\frac{b_{11} - Z_1}{b_{12}}\right) + 1\right]\right\} \qquad (9)$$

The parameters in eq. 9 were fit using that portion of the primary and secondary data (Langenheim, 1962; Reed, 1971) dealing with those significant variables identified in the previous step, resulting in the final production function

$$Y = \exp(11.03 - 0.004Z_3 - 0.3309X_2 - 0.7959Z_7 + 0.3199Z_8 - 0.0994Z_9)$$

$$R^2 = 0.93,\ S_e = 195 \text{ kg ha}^{-1} \qquad (10)$$

where

$$X_2 = \cos\{57.295[\arccos(2726 - Z_1/478) - Z_3]\} + 1$$

Figures 2 and 3 graphically illustrate the model's (eq. 10) forage production predictions for various aspects while varying two variables, elevation (Fig. 2) and stems per hectare (Fig. 3). Different levels of production can exist given different levels of growth factors. In turn, the level of production can be determined by different combinations of site variables. These levels of production can have a wide range where diverse site conditions occur. For example, the figures indicate the effect of elevation and aspect on produc-

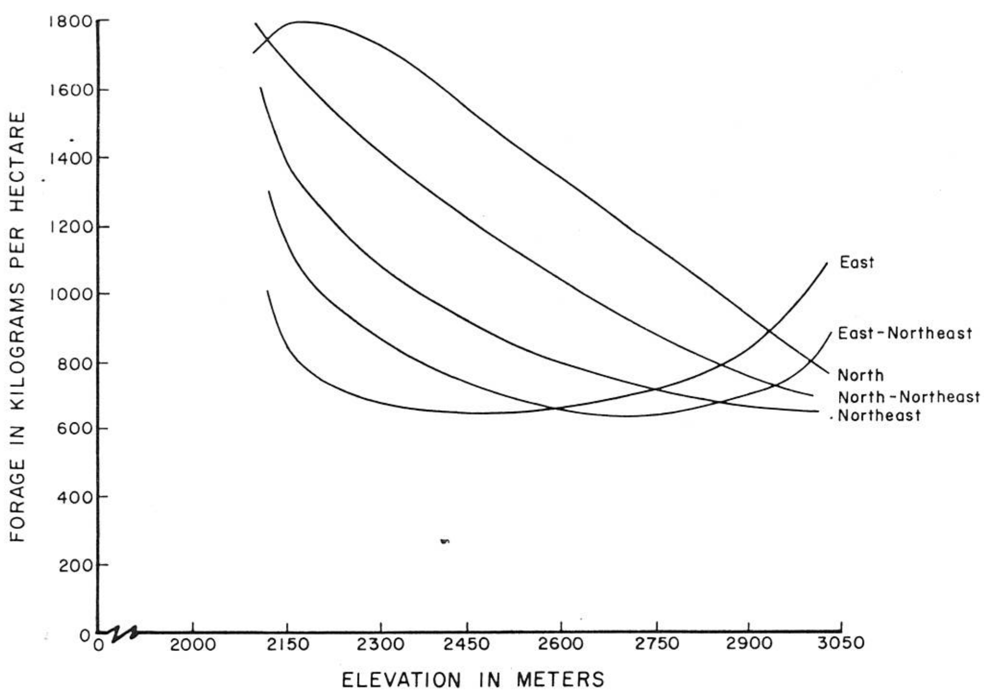

Fig. 2. Forage production as a function of aspect and elevation. South-facing slopes would have curves that mirror these.

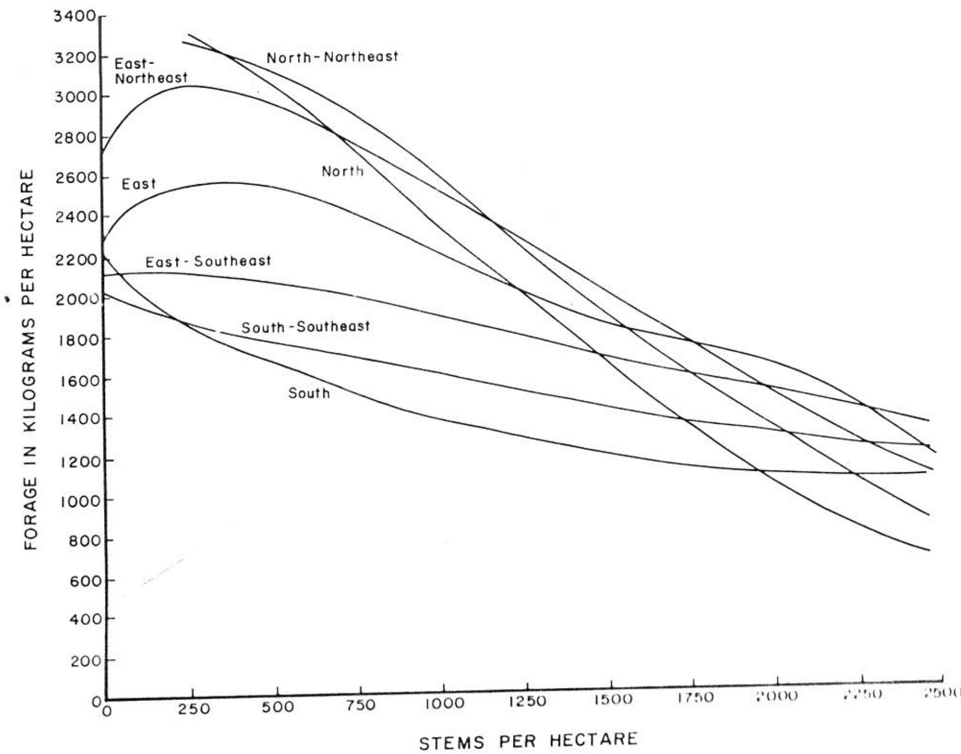

Fig. 3. Forage production as a function of aspect and stems per hectare.

tion. Aspect (Fig. 2) has a much larger influence at lower elevations than at higher elevations, because of its influence on the available moisture growth factor. As elevation increases, the difference in production as a function of aspect is less pronounced. Conversely, as the stems per hectare increase, the production levels become more nearly the same at different aspects (Fig. 3). Here, the overstory vegetation is becoming a major factor influencing the availability of moisture. Numerous other interactions between variables, growth factors and production could be graphed in a similar manner. The model does provide a means of analyzing the interactions between growth factors, site variables and production.

MODEL VERIFICATION

To obtain additional model verification an independent data set was used (Table II). The data were gathered from the same general area as the primary data. Table III shows a comparison of the model predictions and the independent data set measurements. The model seems to accurately predict

TABLE II

Verification data * for testing eq. 10

Site	Aspect (rad)	Elevation (m)	A horizon (Munsel color code)	B horizon (Munsel color code)	Field capacity (g)	Stems (ha)	Forage production (kg ha^{-1})
2	4.19	2743	4	3	10.8	464	1947
4	2.09	2682	3	3	11.8	1186	1189
4	3.40	2652	3	2	14.1	1285	1097
7	3.14	2682	3	3	15.5	62	1961
10	3.53	2743	3	3	10.8	9881	549
14	3.49	2713	3	3	16.2	790	1139
17	4.01	2713	3	3	13.6	470	1711

* These data are given in Woods, (1980).

forage production in the mid-production range, but it is less accurate at high and low production levels. The reasons for this are not clear. The differences could be due to random variation, or possibly the linear form used for stems per hectare gives too much weight to the influence of this variable where large numbers of stems exist. The range in stems per hectare were similar for both the primary data and the verification data except for one very dense stand, site 10 (Table II). This stand contributed heavily to the prediction error.

Given ~~this~~ these new data, the Kolmogorov–Smirnov statistic was used to test the hypothesis as to whether the deviations were within the random variation acceptable for the model ($P = 0.5$, $P = 0.01$) (Birnbaum, 1952). This particular statistic was chosen because of the power of this goodness-of-fit test with small sample sizes (Phillips, 1972). The test (Fig. 4) indicated that the hypothesis was accepted at both levels of significance. While this test does not prove the model is the correct model, it does show that the forage production samples are normally distributed about the model prediction.

TABLE III

Comparison of forage production model predictions and independent data set

Model prediction (kg ha^{-1})	Independent data set measurement (kg ha^{-1})	Difference (kg ha^{-1})
1669	1947	−278
1279	1189	90
1046	1097	−51
2261	1961	300
1101	1139	−38
2573	1711	862
15	549	−534

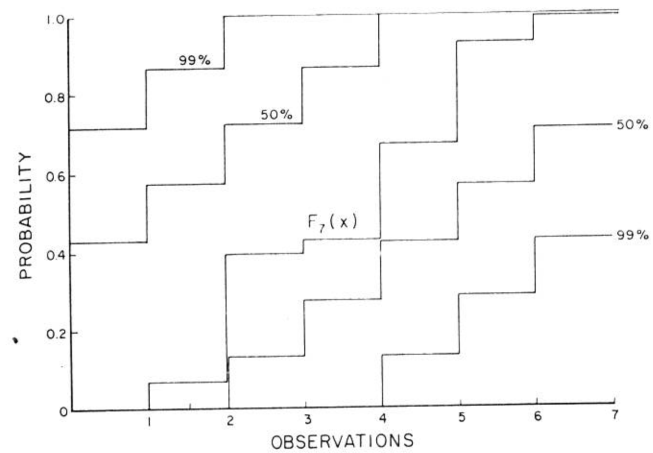

Fig. 4. Two-sided confidence bands for the model prediction (F_7 (X)) using the Kolmogorov–Smirnov statistic at the 50% and 99% confidence levels.

CONCLUSIONS

The approach, as applied to biological production, can successfully develop models which accurately depict the complex interaction within a biophysical system. In this sample, concerning forage production in aspen stands, it serves to point out the importance of elevation, aspect and soil characteristics on moisture and energy growth factors. The final model does provide a meaningful mathematical expression of the growth factor interrelationships and can be useful in analyzing such interactions. The basic approach would seem to be appropriate for application in other cases where similar biological interactions and site diversity exist.

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Announcement

APPLICATION OF ECOLOGICAL MODELLING TO ENVIRONMENTAL MANAGEMENT: Third International Conference on State-of-the Art in Ecological Modelling

The Third International Conference on Ecological Modelling will convene in Colorado at 1:00 p.m. on Monday, May 24, 1982, and will adjourn at noon on Friday, May 28. The theme of this international conference will be "Application of Ecological Modelling to Environmental Management."

Besides technical papers, there will be a strong emphasis on case studies, which will be presented briefly during the concurrent technical sessions and in more detail during the "Poster Displays". These case studies could consist of 2–5 individual papers, with each paper describing some particular aspect of the case study. Abstracts of 200–500 words should be forwarded to either Prof. Gaylord V. Skogerboe or Prof. William K. Lauenroth, Natural Resources Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523, U.S.A. These abstracts should be received by December 15, 1981. It would be helpful if all of the abstracts for a case study were mailed in a single envelope; or if mailed separately, the particular case study should be clearly indicated. Authors will be notified in January, 1982. The complete paper will be requested by May 1, 1982.

The technical subject areas proposed for this conference are:

- Model identification, development, parameter estimates, stability, validation, and verification.
- Model applications to lake systems.
- Model applications to river systems.
- Model applications to coastal estuaries and bays.
- Model applications to fishery problems.
- Model applications to wetlands.
- Model applications to forests.
- Model applications to deserts.
- Model applications to tundra.
- Model applications to grasslands.
- Model applications to shrublands.
- Model applications to croplands.
- Case studies, such as the Baltic Sea, Great Lakes, Rhine River, Upper Nile Lake System, North Sea, Delaware Bay, Niepolomice Forest (Poland), Kawatabi Grassland (Japan), Great Plains Agro-ecosystems (U.S.A.), The Moore House National Reserve (U.K.), Lamto Savanna (Ivory Coast), etc.